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THE SKULL OF THE CROCODILE

A Manual for Students

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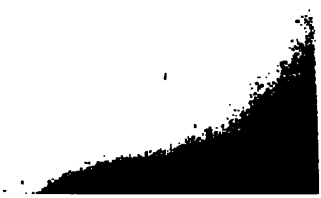

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THE SKULL OF THE

STUDIES IN COMPARATIVE ANATOMY.—No. I.

THE SKULL OF THE CROCODILE

A Manual for Students

BY

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THE SKULL OF THE CROCODILE.

PRELIMINARY INSTRUCTIONS.

CROCODILES' skulls can be purchased without difficulty in most large towns, especially in sea-ports. Those about a foot long are most convenient for study. Two examples at least should be procured.

Saw one of the skulls through longitudinally, keeping about one-eighth of an inch from the middle line. Make another section parallel to the first through the centre of the supra-temporal fossa. Divide the other half of the skull transversely at the junction of the opisthotic and epiotic bones in the wall of the cranial cavity.

The other skull is to be disarticulated. The process is troublesome, but not too difficult if much patience and little force are used. Begin at the end of the snout by separating and then removing the premaxillaries. A mallet and wooden wedges will be required.

The species most commonly met with in England are *Alligator Mississipiensis* (*lucius*) and *Crocodilus Americanus* (*acutus*). One example of each should be procured, if possible, besides one of *Gavialis Gangeticus*, and kept entire for comparison.

GENERAL VIEW OF THE CROCODILIAN SKULL.

As to its general form, the skull of crocodiles is characterised by its flat superior and palatal surfaces, its vertical occipital surface, the great length of the gape and of the dental alveoli, and

the removal of the mandibular articulation to a point behind the occiput.

On the fore part of the upper surface of the skull are to be observed the external nares, forming a single aperture in the dry skulls of *Caiman*, *Jacare*, *Crocodilus*, and *Gavialis*, but divided by median processes of the nasal bones in *Alligator*. Further back are the orbits, which are complete, and separated from each other by the frontal bone. A process of the post-frontal divides the orbit from the lateral temporal fossa, a cavity which in the living animal is largely filled by muscle. The back of the skull is mainly occupied by a flat, square, bony roof, perforated by the two supra-temporal fossæ. The central part protects the small brain. Below the outer edge of the bony roof will be found the auditory meatus. The postero-lateral angles of the skull are occupied by the quadrate bones, which project beyond the occiput, and serve to suspend the mandible.

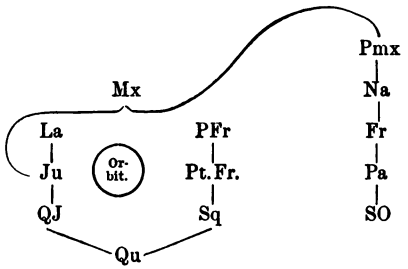
On the posterior or occipital surface will be found the foramen magnum, through which the spinal cord passes into the skull, and immediately below the foramen the rounded condyle formed by the basi-occipital bone. The extremity of the quadrate appears in this view also, and below it the pterygoid plate, ending outwards in a thickened edge, which is tipped with cartilage in a fresh skull, and plays against the inner surface of the mandible.

The bony palate is formed by the following pairs of bones, which meet along the middle line in order as enumerated, from before backwards: (1) premaxillæ, (2) maxillæ, (3) palatals, (4) pterygoids. The exclusion of the vomers [1] and the union in pairs of the maxillæ, palatals and pterygoids are unusual. The posterior nares are remarkably far back, and open in the pterygoids. In the suture between the premaxillæ is a foramen, named from an erroneous interpretation the *foramen incisivum*; it is covered in by membrane in a fresh skull. External to the palatals are large oval spaces, the palatal foramina; in the living animal they are closed by membrane,[1] and the cavity to which they lead (part of the pterygoid fossa) is occupied

[1] The vomers are visible, to a small extent, between the premaxillæ and maxillæ of *Jacare*; and between the maxillæ and palatals of *Tomistoma*.

by a muscular mass. The postero-external border of the foramina is formed by the transpalatine[2] bone (*os transverse* of Cuvier).

The arrangement of the inferior bones of the skull is peculiar to Crocodilia, but the plan of the superior cranial and facial bones is fairly typical, not only of reptiles, but of many lower vertebrates. Diagrammatically, the disposition is as follows:—



The superior cranial bones, and the outer surface of the mandible, as is not uncommonly the case with the subcutaneous bones of cold-blooded vertebrates, are deeply pitted. This feature is conspicuous also in the extinct Labyrinthodontia, which have many superficial points of resemblance to Crocodilia.

The cranial bones (and this also holds good of most Labyrinthodonts) are ossified from the time that the animal leaves the egg. Not only are the sutures closed before the end of the embryonic stage, but the frontals and parietals, originally paired bones, are firmly ankylosed, each to its fellow. This rapid completion of a solid and compact skull does not preclude the further growth of each separate bone. The skull increases indefinitely up to the very end of life, retaining all the time its accurately closed sutures. Growth takes place, as in the echinus shell, by means of continual additions to all the borders of each ossification, a mode of enlargement compatible with great changes in the form of the skull. The face increases more rapidly than the brain-case, and the orbits become relatively further from the

[1] Cuvier, or his editor, erroneously says (*Leçons D'Anat. Comp.*, Leç. viii. Art. 3) that they give passage to the temporal muscles.

[2] Parker, "Development of the Skull of the Salmon," *Phil. Trans.*, vol. 163, pt. i., p. 97.

snout. Early protection from injury is thus reconciled with unlimited growth, and such changes of proportion as are physiologically needful.

Each ramus of the mandible consists of the six pieces hereafter enumerated. The post-articular process is longer than in any other animal; there is no coronoid process. Union of the two rami is effected by the dentary bones alone, except in *Gavialidæ*, where the splenials enter into the symphysis. Towards the articular end of the mandible are seen, on the outer side, the external mandibular foramen; on the inner side, the mandibular fossa, and further forward, the internal mandibular foramen. The first of these three openings is closed by a strong tendinous membrane, which gives attachment to muscles by its inner surface. The biting muscles are inserted into the mandibular fossa, while the internal mandibular foramen, though nearly closed by membrane, serves for the passage of vessels and nerves.

The following cranial characters enter into the definition of Crocodilia :—

The quadrate is immovably fixed among the cranial bones, as in Chelonia and *Hatteria*. There is a distinct transverse or transpalatine bone. The presphenoid is not ossified, and no orbito-sphenoids have been identified with certainty. The maxillæ, palatals, and pterygoids meet in the middle line in all recent Crocodilia, and the vomers are excluded from the palate.[1] The posterior nares are far back (in recent Crocodilia) and are bounded by the pterygoids. The premaxillæ, maxillæ, and dentary piece of the mandible are the only dentigerous bones. The mandible has a long post-articular process; the coronoid is not elevated.

The following cranial characters are available for the subdivision of Crocodilia into families and genera :—

ALLIGATORIDÆ.—The first and fourth mandibular teeth bite into pits or perforations in the upper jaw.

Alligator.—Nasal bones prolonged so as to separate the anterior nares.

Caiman.—Supra-temporal fossæ obliterated.

Jacare.—Vomers appearing in the palate.

[1] Except in *Jacare* and *Tomistoma*.

CROCODILIDÆ.—The first mandibular tooth bites into a pit or perforation, the fourth into a lateral notch in the upper jaw.

Crocodilus.

GAVIALIDÆ.—Both the first and the fourth mandibular teeth bite into lateral notches in the upper jaw. Splenials enter into mandibular symphysis.

Tomistoma (*Rhynchosuchus*).—Mandibular symphysis extending to the fifteenth tooth. Premaxillæ hardly expanded. Vomers appearing in the palate.

Gavialis.—Mandibular symphysis extending to the twenty-third or twenty-fourth tooth. Premaxillæ and end of mandible conspicuously expanded.

SKETCH OF THE DEVELOPMENT OF THE CROCODILIAN SKULL.

The cranium, when first recognizable as such, consists of an irregular plate or shallow cup of hyaline cartilage, incomplete above, and occupying the position afterwards allotted to the basi-occipital and basi-sphenoid bones in the floor of the brain-case. This cartilaginous plate is known as the *basis cranii*, or *investing mass*, from the way in which it surrounds, as in a sheath, the tapering end of the notochord; it represents that part of the embryo, which, further back, gives rise to the first rudiments of vertebræ.

The posterior end of the investing mass rises on either side into a broad flat process, and these processes are completed above by a still broader transverse plate. The arch thus formed encircles the spinal cord, and prefigures the occipital segment. Further forward, the sphenoidal part of the investing mass sends upwards and forwards a broad wing on each side; these, when ossified, become the alisphenoids. Laterally, between the occipital and alisphenoidal ascending processes and a little behind the end of the notochord, lie the *periotic capsules*, auditory sacs inclosed in the investing mass, and replaced in the adult skull by the periotic bones.

In front, the investing mass is attached to two nearly horizontal processes, the *trabeculæ cranii*, which pass forwards and downwards, diverging at first, but quickly reuniting, so as to

enclose a somewhat triangular space (the *pituitary space*), which is at first closed below by the mucous membrane of the mouth. The reunited trabeculæ give off a vertical median (*ethmo-presphenoid*) plate, the hinder part of which forms the cartilaginous interorbital septum, and the fore part a partition between the nasal sacs. Continuing to grow, the ethmo-presphenoid plate gives off lateral laminæ from its summit, which roof in the fore part of the orbits behind, and the nasal sacs in front, taking the place of the prefrontal bones and turbinal cartilages of the adult skull.

The roof of the skull is ultimately completed by ossifications in membrane, which are united by suture before the young crocodile leaves the egg.

The remainder of the skull is contributed by paired appendages developed in the visceral arches.[1] Meckel's cartilage, developed in the first post-oral arch, divides into distal and proximal parts, which are ultimately connected by an articulation. The proximal end, which is adjacent to the auditory capsule, yields the quadrate bone, and sends forward a maxillo-palatine process, or secondary arch, which is subsequently divisible into an external (maxillary) and an internal (palato-pterygoid) tract. Lastly, the mandibular rod, or distal part of Meckel's cartilage, undergoes segmentation; its proximal end, when ossified, becomes the articular bone, while the distal end remains unossified, but is completely invested by the five membrane-bones of the mandibular ramus.

The second postoral arch furnishes the hyoid apparatus, which in Crocodilia is simple and imperfectly ossified. The succeeding (branchial) arches are not represented, so far as is certainly known, in the adult crocodile, or in such embryos as have been examined.

Cartilage-bones of the Crocodilian Skull.

(Names in square brackets refer to elements which are not ossified. ? means that the identification is doubtful.)

[1] It has been contended that the trabeculæ are serially homologous with these paired appendages, but the point is not yet established.

Basi-occipital. Ex-occipital. Supra-occipital. Basi-sphenoid. Alisphenoid. Orbito-sphenoid? [Presphenoid. Ethmoid. Turbinals.] Pro-otic. Epiotic. Opisthotic. Pre-frontal. Quadrate. Articular. Pterygoid. Palatal.

Membrane-bones of the Crocodilian Skull.

Dermo-supra-occipital. Parietal. Squamosal. Frontal. Post-frontal. Lachrymal. Nasal. Premaxilla. Maxilla. Vomer. Jugal. Quadrato-jugal. Transpalatine. Dentary. Angular. Surangular. Splenial. Coronoid.

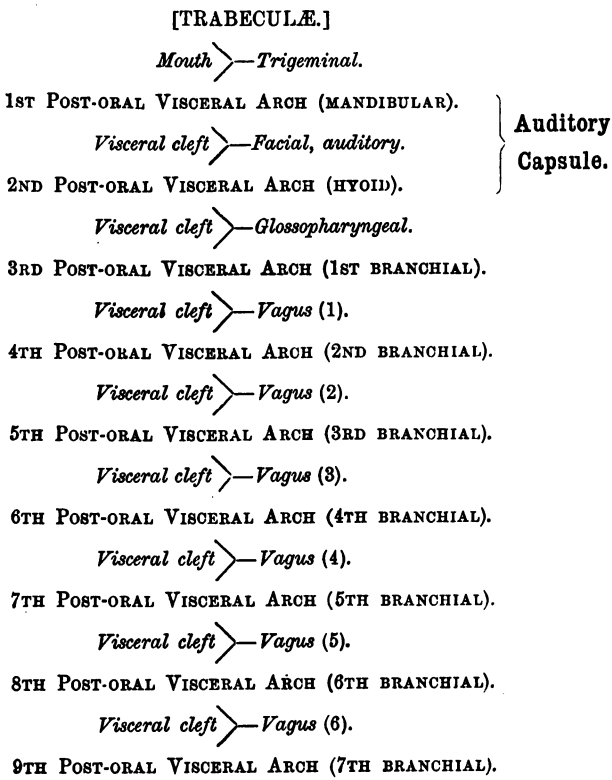
The development of any one skull can only be understood by comparison with others. By comparison the inconstant features are eliminated, and some notion of the primitive skull obtained. The result, as yet most incomplete, of a long series of such investigations yields the visceral skeleton as the possible primitive skull—a structure certainly of high antiquity and generality.

We may regard the visceral skeleton as the fore part of the axial skeleton. It is intersected by the notochord, and provided with a long series of appendages, which are apparently comparable to what in the hinder part of the body are known as ribs and inferior vertebral arches. The visceral arches are separated from each other by clefts (the visceral clefts), which open into the pharynx and may bear gills. No representation of the superior arches can be traced in advance of the occipital segment of the skull, and the notochord ends at or near the same point.

Anterior to the occipital segment the visceral skeleton becomes early complicated with the auditory capsules, and in advance of these the inferior arches also cease to be capable of recognition. It is still an unsettled question whether the trabeculæ represent a pair of visceral arches or not. The undoubted arches are all post-oral; they may amount to as many as nine, each of which is known to bear gills in some animal, and in some stage of development.

The relation of the cranial nerves to the visceral skeleton suggests that (in the post-oral region, at least) each pair was primitively distributed to the contiguous surfaces of two arches.

Thus, the trigeminal appears to be typically distributed to the sides of the oral cleft; the facial and auditory (probably representing a single pair) to the cleft between the mandible and hyoid: the glosso-pharyngeal to the cleft between the hyoid and first branchial arch; while the succeeding nerves which in the higher vertebrates are aggregated, and known collectively as the vagus, or pneumogastric, appear to have been primitively distributed to the posterior branchial clefts. In the appended diagram these relations are indicated; and the arrangement, though imperfect, approximately represents the inferior arches of the visceral skeleton. All the nerves here mentioned are budded out from the spinal cord behind that part of the posterior cerebral vesicle which ultimately forms the cerebellum; in the adult they all pass into the medulla oblongata or spinal cord.


[TRABECULÆ.]
Mouth — Trigeminal.
1st Post-oral Visceral Arch (mandibular).
Visceral cleft — Facial, auditory.
2nd Post-oral Visceral Arch (hyoid).
Auditory Capsule.
Visceral cleft — Glossopharyngeal.
3rd Post-oral Visceral Arch (1st branchial).
Visceral cleft — Vagus (1).
4th Post-oral Visceral Arch (2nd branchial).
Visceral cleft — Vagus (2).
5th Post-oral Visceral Arch (3rd branchial).
Visceral cleft — Vagus (3).
6th Post-oral Visceral Arch (4th branchial).
Visceral cleft — Vagus (4).
7th Post-oral Visceral Arch (5th branchial).
Visceral cleft — Vagus (5).
8th Post-oral Visceral Arch (6th branchial).
Visceral cleft — Vagus (6).
9th Post-oral Visceral Arch (7th branchial).

Bones of the Skull in Detail.

The Occipital Segment in the skull of the crocodile consists of four permanently distinct bones. Three of these surround the foramen magnum, through which the spinal cord enters the brain-case; the fourth lies above the foramen at a short distance.

The basi-occipital is the lowest of these four bones. It furnishes nearly the whole of the occipital condyle,[1] and enters above into the foramen magnum as well as into the floor of the brain-case. The condyle itself is single, and nearly uniformly rounded, but with a slight median groove. On the upper surface of the basi-occipital are two rough surfaces inclined outwards, which articulate with the ex-occipitals, and between these is a smooth surface transversely concave and longitudinally convex, which expands and deepens anteriorly. Upon this smooth surface rests the spinal cord, and in the enlarged cavity, which constitutes the posterior half of the floor of the brain-case, the medulla oblongata is lodged. The anterior surface of the basi-occipital is nearly vertical, and covered with irregular splinters of bone. The posterior surface of the basi-sphenoid has a similar character, and the two bones are thus firmly articulated. Half-way down this articular surface in either bone is seen the entrance to a canal, which passes below into a median vertical groove. Placing the two bones together in the natural position, it is seen that the canal is at its mouth round and single, opening downwards at some distance below the occipital condyle; that it rapidly contracts as it enters the skull, passing upwards in the spheno-occipital suture; and that it at length divides into two branches, one of which enters the basi-occipital, and the other the basi-sphenoid bone. A bristle passed into the posterior of these two branches may be caused to emerge at a large oval foramen situated at the junction of the anterior, superior, and lateral surfaces of the basi-occipital. Passing thus into the ex-occipital, the canal communicates ultimately with the tympanic cavity. At the junction of the basi-occipital and ex-occipital bones the canal is seen to expand

[1] The occipital condyle is single and situated beneath the foramen magnum in all reptiles and birds. In the turtle it has a trefoil shape, and is constituted by the basi-occipital and the two ex-occipitals in nearly equal proportions.

into a sinus (the "rhomboidal sinus" of Owen), and here it receives on each side a smaller lateral canal. The grooves which, when united, form this, the "posterior lateral canal," pass up in the spheno-occipital suture in some species; in others, the canal commences below in the basi-sphenoid bone, immediately anterior to the suture, and only grooves the basi-occipital close to the rhomboidal sinus. The median and lateral canals here mentioned form part of a complicated system of Eustachian passages, whose remaining extensions and connections will be noticed hereafter. On the under-side of the basi-occipital, anterior to the condyle, there is usually present a small foramen, which gives passage to a vein from the substance of the bone. Below this a strong median ridge appears, which divides the surfaces of attachment of the *recti capitis antici* and *laterales* muscles.

The basi-occipital articulates with four bones, viz., with the basi-sphenoid and ex-occipitals by suture, and with the atlas by diarthrosis.

The ex-occipitals form the lateral elements of the occipital segment. They constitute about six-sevenths of the boundary of the foramen magnum, a small strip below being furnished by the basi-occipital. Above, the two ex-occipitals meet in the middle line, and thus exclude the supra-occipital from the foramen. This suture is the only place where the two ex-occipitals touch. Its proportionate vertical extent varies according to the species, being ordinarily greater in the true crocodiles than in the alligators. The posterior surface of the ex-occipitals occupies the greater part of the occipital tract in the complete skull. It presents a smooth surface for muscular attachment, extending laterally to the quadrate bone, a series of foramina external and inferior to the foramen magnum, and a triangular descending process which is locked in between the basi-occipital internally, and the basi-sphenoid in front. The muscles attached to the posterior surface of the bone are:—part of *complexus, trachelo-mastoideus* and *sterno-mastoideus*, each insertion being inferior and somewhat external to the preceding in the above list. The foramina visible on the posterior surface of the ex-occipital are five in number. Three of these are situated in a nearly horizontal line external to the roots of the condyle, and in order outwards

give passage to the hypoglossal nerve, a small vein from the tympanic cavity, and the pneumogastric nerve. In the true crocodiles the last two foramina unite. Lower down is the entrance of the internal carotid artery; lastly, between the ex-occipital and the quadrate is a large foramen for the facial nerve, a branch of the jugular vein, and an artery. On the internal surface of the ex-occipital we observe the exceedingly rough horizontal surface for articulation with the basi-occipital, and the inner face of the descending process, which adjoins the same bone. In the angle between these two surfaces is an opening into the rhomboidal sinus of the Eustachian passages, exposed by the separation of the ex-occipital and basi-occipital. The concave surface immediately above the rough horizontal suture forms with the other ex-occipital and the basi-occipital the inner wall of the passage for the spinal cord. In this surface, at about the junction of the middle and lower thirds, are seen two foramina. The anterior of these gives exit to a vein which joins that from the tympanic cavity already mentioned; the posterior is for the passage of the hypoglossal nerve. Anterior to these two foramina a long slit is seen, inclined at an angle of about 45°. Through this the eighth pair of nerves quits the skull. In front of this slit a thin plate of bone is seen, which, together with an excavated mass of bone superior and external to it, forms a distinct osseous element of the skull, the opisthotic bone, though in the adult crocodile it is so firmly united with the ex-occipital that no suture is visible. The opisthotic will be described with the other periotic bones. Not only the opisthotic but the ex-occipital proper is excavated by air-cells, which communicate with the tympanic cavity and with the Eustachian passages. Besides the air-canals and foramina for nerves, the ex-occipital is transversed by the internal carotid artery, whose conspicuous channel may be traced by a bristle from the entrance on the posterior surface of the bone nearly vertically upward to a point a little external to the rhomboidal sinus. After emerging from the ex-occipital the artery is continued across the lower part of the tympanic cavity, being in this part of its course unprotected by bone; it quickly passes downwards into the basi-sphenoid, and emerges at the back part of the pituitary fossa. In front, the ex-occipital presents a rough,

splintered surface for articulation with the quadrate bone; above it unites with the supra-occipital by the surface which slopes downwards towards the middle line; and external to this suture it is articulated with the squamosal by a narrow surface of considerable lateral extent. The ex-occipital is, in all, connected with six bones, namely, the basi-occipital, the other ex-occipital, the supra-occipital, the quadrate, the squamosal, and basi-sphenoid.

The supra-occipital is an unpaired median bone, which occupies a small space at the upper part of the back of the skull, and in some species of Crocodilia, presents itself on the upper surface also.[1] In front the supra-occipital is closely united with the epiotic, just as the ex-occipital is with the opisthotic. When completely detached, the supra-occipital consists of a vertically placed triangular plate, whose apex is directed downwards. The roof of the posterior half of the cranial cavity as well as the large air-cells which communicate on either side with the tympanic cavity, are contributed by the epiotics; and the whole is surmounted by a membrane-bone, which appears to be a dismemberment of the parietal. On the smooth posterior surface of the supra-occipital are two fossæ, partly divided by a median ridge. Here are inserted *splenius* and the upper fibres of *complexus*. On the external superior angles of the same posterior plate are slightly-roughened surfaces, looking obliquely upwards. To these surfaces are attached small masses of cartilage, which are interposed between the supra-occipital below and the squamosal and parietal above. Here the temporal artery passes into the tympanic cavity. The supra-occipital articulates with six bones, viz., the two ex-occipitals, parietals, and epiotics.

There is an obvious successional correspondence of the occipital segment with the vertebræ. The condyle of the reptile is in the line of centra; the ex-occipitals are lateral processes answering to neurapophyses; the supra-occipital is, in position at least, a neural spine. The cranio-spinal mass is related to these parts of the occipital segment just as to the essential constituents of the vertebra, and the primary elements of both the vertebral and occipital segments are similarly developed in

[1] Or appears to do so, being united with a membrane-bone which forms a kind of post-parietal (*dermo-supra-occipital*).

cartilage, and ossified from separate centres. It is noticeable, however, that from the very first appearance of its cartilaginous rudiment, the occipital segment is not a true vertebra, but a portion of the skull. No part of the occipital bones pre-exists as a "proto-vertebra," such as indicates in the embryo the future place of every vertebral segment. The facts of structure and relation would justify us in regarding the occipital segment as a vertebra, but the facts of development tell us that from the time that skull and vertebral column become distinguishable the occipital segment belongs to the skull only.

The vertical position of the occipital bones, and the complete restriction of their exposed surfaces to the posterior face of the skull are peculiar features of Crocodilia.

The BASI-SPHENOID lies anterior to the basi-occipital, and is the succeeding segment of the cranio-facial axis. It is wedge-like in form, the converging sides being nearly vertical, and the inferior surface being much narrower posteriorly than the superior.

The superior surface presents two cavities: an anterior, which receives the pituitary body, and a posterior, which forms about one-half of the floor of the brain-case. The pituitary fossa, or *sella turcica*, is of large size and deeply excavated, extending for a considerable distance beneath the floor of the brain-case. Far back in the fossa are seen the two openings by which the carotid arteries enter. The overhanging roof terminates in front in two clinoid processes. As it advances beyond the sides of the fossa, an acute angle is left on each side unoccupied by bone. In the wall of the fossa, at or near to the apex of this angle, are seen foramina which lead to the floor of the brain-case, and serve for the passage of the sixth pair of nerves. The sphenoidal portion of the floor of the brain-case presents in its anterior half the inclined surface upon which the medulla oblongata lies. Immediately behind this, and close to the middle line are a pair of oval depressions not indicated on the corresponding part of the brain. External to these, and rather in advance, are the foramina through which the sixth pair of nerves leaves the brain-case. The smooth cranial surface of the basi-sphenoid is bordered by rough articular surfaces. Just behind the pituitary fossa are two oval spaces, upon which rest the buttresses of the alisphe-

noid. Further back is the articulation of the pro-otic, and external to this, the bony canal for the carotid artery. On tracing this forward by inserting a bristle, it is seen to emerge at the back of the pituitary fossa. From this point forward the artery is not inclosed in a bony canal. The anterior tympanic passage takes a downward direction immediately in front of the carotid canal. The rough posterior surface of the basi-sphenoid articulates with the basi-occipital. The anterior branch of the common Eustachian passage is here seen passing upwards and inwards into the body of the bone. Its course may be followed (in large examples by bristles, in smaller ones by injection), and the passage will be found to lead to the side of the basi-sphenoid. No opening exists at this point in the connected skull, but the canal turns upwards into the same bone, passing thence into the pro-otic, and ending in the anterior part of the tympanic cavity. Laterally, the basi-sphenoid presents two smooth surfaces separated by a biconcave rough surface. With the upper part of this rough space three bones articulate, viz., the alisphenoid anteriorly, the pro-otic in the middle, and the quadrate for a small space behind. Below the narrowed part of the articular surface the pterygoid is attached. The lower extremity of the internal ear, in which the cochlea is lodged, is partly visible, being bounded by the three articulations described. Of the two smooth surfaces the foremost constitutes the bony part of the orbital septum, while the posterior appears outside the cranium in the pterygoid fossa, surrounded by the basi-occipital, the quadrate, and the pterygoid.

The basi-sphenoid articulates with the following bones:—basi-occipital, ex-occipital (at the superior external angle of the cerebral surface), quadrate, pro-otic, alisphenoid and pterygoid.

The alisphenoid is attached to the basi-sphenoid by a hemispherical facet immediately behind the pituitary fossa, and also by a triangular tongue of bone which passes a short distance down the side of the basi-sphenoid. The two alisphenoids join in front by a narrow isthmus anterior to the pituitary fossa, diverge to form the bony edge of the optic foramina, and are again united in front of that aperture as far as their anterior extremities, or nearly so. The optic aperture in the dry skull appears as a rather large and somewhat irregular median

opening. A large part of this space is occupied in the fresh specimen by cartilage, through which the foramina for the passage of the optic nerves are pierced. Examined from within, the alisphenoid presents a large concavity, which receives the cerebral hemispheres. The fore part of the brain-case is largely bounded by the two alisphenoids, the base being formed by the basi-sphenoid, and the roof by the parietal and frontal bones. The cavity gradually contracts forwards, until it terminates in the olfactory canal, which is continued forward along the underside of the frontal bone, and as far as the descending process of the pre-frontal.

Along the middle line of the alisphenoid, and on its superior aspect, we observe in order from before backwards the principal articular surface for the other alisphenoid, the optic aperture, a second and narrower articular surface for the other alisphenoid, the upper edge of a fissure, visible only in the dry skull, which lies between the inner margin of the alisphenoid and the external lip of the pituitary fossa; lastly, the strong parapet of bone, which rests upon the basi-sphenoid, and the triangular slip which passes down on its outer side.

Through the membrane which closes the fissure the third nerve and the orbital artery (Rathke) make their exit, while the sixth, emerging from its bony canal in the wall of the pituitary fossa, finally quits the skull through this opening.

In the cartilaginous interorbital septum near the optic foramina occur two small ossifications which Stannius[1] regards as orbito-sphenoids, and attached to them below a minute impaired bony slip, which he considers the representative of the presphenoid.

Externally the alisphenoid presents two surfaces separated by a strong ridge of bone, which passes from below upwards and forwards. The anterior of these surfaces looks into the orbit; the posterior into the supra-temporal fossa. The ridge of bone passes upwards into a single or double articular process which abuts upon a concavity formed in the united frontal and post-frontal bones. The quadrate is almost in contact with the posterior head of this articular process, but the bones are separated by cartilage except in fully adult skulls. In front of

[1] *Zootomie der Amphibien*, p. 56.

the process just mentioned the alisphenoid joins the frontal; behind, it articulates with the parietal.

Viewed from behind the alisphenoid exhibits the notch which forms the anterior boundary of the foramen ovale. Above and below are articular surfaces, the former for the pro-otic internally and the quadrate externally; the latter for the basi-sphenoid (as has already been mentioned) internally, the pro-otic (in some skulls) in the centre, and the pterygoid externally. The foramen ovale is bounded by the alisphenoid in front and the pro-otic above, beneath and behind. It gives passage to the three divisions of the trigeminal or fifth nerve; a fact of some morphological importance, upon which the homological determination of several bones in the crocodilian skull partly rests. External to the front or alisphenoidal border of the foramen ovale a splinter of bone arches over an oval slit in the wall of the alisphenoid. Through this slit pass the first division of the fifth nerve (forwards, after emerging from the foramen ovale) and a recurrent branch of the internal carotid (backwards, from the sella turcica.)

The alisphenoid is articulated with eight bones, viz., the basi-sphenoid, frontal, parietal, quadrate, pro-otic, post-frontal, pterygoid, and fellow alisphenoid.

The basi-cranial axis of the crocodilian skull comprises only two continuous and uncontroverted segments. Passing by the pre-sphenoid of Stannius as of small structural importance, and open to question, we find the basi-occipital and basi-sphenoid constituting the foundations of the cranial chamber. Each has its pair of lateral appendages. These are the ex-occipital and basi-alisphenoids, which, though not exclusively, form the actual parietes of the chamber. The orbito-sphenoids of Stannius are equally hypothetical with the pre-sphenoid, and, whatever be their homological character, take no share in inclosing the cranial cavity. Only the posterior part of the vault is completed above by a cartilage-bone, the super-occipital, for the parietal and frontal, which arch over the sphenoidal segment, are developed in membrane, and have a quite different morphological significance from the primitive cranial elements. Were the brain-case to be restored by putting in position the disarticulated bones, it would be still most incomplete, if no bones

were inserted but the constituent parts of the occipital and sphenoidal segments. The cranial cavity would remain entirely unroofed, and the parietes would be defective in nearly one-half of their longitudinal extent. The membrane bones which overarch the cranium will be described subsequently; there remain three cranial cartilage-bones, which complete the brain-case laterally. These three bones are named PERIOTIC, because they invest the organ of hearing, and from their relative position they have been severally designated pro-otic, epiotic and opisthotic. Though originally distinct, and ossified from separate centres, they do not all continue independent. In the crocodile the epiotic is early united with the supra-occipital, and the opisthotic with the ex-occipital; the pro-otic alone remains separable throughout life.[1]

The relations of the periotic bones to the organ of hearing and to each other can only be understood after the study of sections along the various planes already described (p. 1).

Upon the cerebral surface the periotic bones are easily traced. Each of them contributes to form a conspicuous rounded or pyramidal projection above and external to the occipito-sphenoidal suture. The walls of this projection are thin and translucent; they contain the vestibule of the internal ear, and unite by a Y-shaped suture. The descending branch marks the boundary between the pro-otic and opisthotic bones; the upper and bent suture divides the epiotic from the pro-otic in front, and from the opisthotic behind. The sutures which define the cerebral extent of the pro-otic are all persistent. The superior edge of the bone is continued forward from its junction with the epiotic as far as the posterior edge of the parietal; then the outline, bounded anteriorly by the alisphenoid, descends perpendicularly to the top of the foramen ovale. The boundary between the pro-otic and basi-sphenoid passes longitudinally from the foramen ovale to the occipito-sphenoidal suture. A short and irregular vertical fissure divides the pro-otic from the ex-occipital and opisthotic. The inferior cerebral

[1] In the turtle, the opisthotic remains permanently distinct. "In birds, the three periotic bones anchylose with one another, as well as with the adjacent supra-occipital and ex-occipital, so completely, that even the Y-shaped suture becomes obliterated" (Huxley).

border of the epiotic has already been traced: above, the bone is anchylosed with the supra-occipital at an early stage, and its extent in this direction cannot therefore be seen in any but embryonic skulls. It includes at least so much of the under surface of the cranial roof as incloses below the large oval aperture of communication between the tympanic cavities. The opisthotic comprises the remaining or posterior third of the vestibular projection and a small part of the adjacent wall of the canal for the spinal cord.

The following details respecting the bony framework of the ear can be traced in sections made in the manner described.

The meatus auditorius externus opens on the side of the head in a fossa (the lateral temporal) of considerable extent, which is bounded mainly by the squamosal and the quadrate. In the anterior part of this fossa the quadrate is excavated by a canal[1] of oval section, which joins the tympanic cavity. Another canal, bounded by the ex-occipital behind and the quadrate in front, opens upon the posterior wall of the external auditory meatus, and transmits vessels and a large branch of the facial nerve. The lateral temporal fossa rapidly contracts to the membrana tympani. Only the anterior rim of the frame for this membrane is formed by bone (the quadrate); about one-third of the circumference being deficient in the dry skull. The plane of the membrana tympani looks outwards and upwards, being inclined at an angle of about 45°.

The tympanic cavity is bounded by the quadrate, pro-otic and epiotic bones anteriorly; by the quadrate, ex-occipital, and epiotic posteriorly; and by the periotic bones internally; its floor is mainly formed by the quadrate. The posterior wall is seen to be divided into three parts by a nearly horizontal ledge of bone proceeding from the ex-occipital, and at a higher level by a parallel ledge given off by the ex-occipital and opisthotic. In the lowest division of this surface the carotid canal is seen to emerge just beneath the horizontal plate. The middle space serves as a communication between the membrana tympani and the internal ear; it is not occupied, as in mammalia, by a chain of ossicles, but a long curved stapes or columella, attached at one end by an intervening cartilage to the membrana tympani,

[1] Wanting in *Gavialis*.

and expanded at the other so as to correspond nearly with the aperture of the fenestra ovalis, extends across, and transmits vibrations.

The upper division of the posterior surface of the tympanic cavity is occupied by air-cells, incompletely separated from each other by bars of bone. The communication with the opposite tympanic cavity through the supra-occipital and epiotic is readily seen in the transverse section.

The anterior wall of the cavity is displayed in the other half of the transversly divided skull. We see here the well-marked anterior rim of the bony frame for the membrana tympani; just beneath it the previously-mentioned canal passing outwards and forwards; a canal passing perpendicularly downwards in the pro-otic bone and terminating in the pterygoid fossa, through which passes a nerve (recurrent branch of the fifth joining the facial); the air-cells and communicating passage through the supra-occipital and epiotic, and lastly, the descending canal in the inferior and internal angle, beneath the cochlea, through

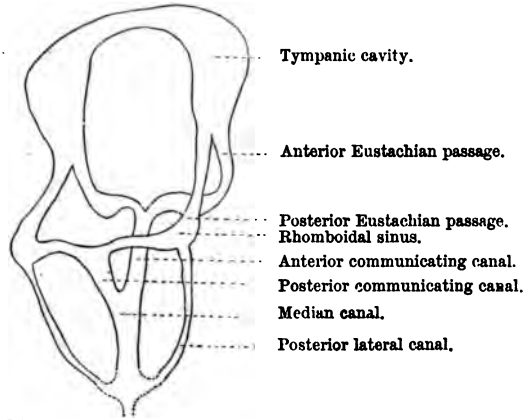


Diagram of Eustachian Passages of Crocodile. (No attempt is made to represent the intricate form of the tympanic cavity.)

which the internal carotid artery quits the cavity. Between the carotid foramina, which open, the one upon the posterior and the other upon the anterior wall of the tympanic cavity, the artery is uninclosed by bone. Its emergence in the pituitary fossa has already been noticed.

The openings of the Eustachian passages into the tympanic

cavity have not yet been mentioned. It will be convenient to describe them with reference to the entire system of communication between the pharynx and tympanum, which in Crocodilia manifests a remarkable and unparalleled complexity.

The median Eustachian canal passes upwards in the occipito-sphenoidal suture, and divides into an anterior and a posterior communicating canal. The posterior communicating canal traverses the basi-occipital for a short distance, and then divides into two lateral branches, the posterior Eustachian passages. Each of these is joined by the nearly vertical lateral canal, which passes upwards in the occipito-sphenoidal suture. Close to the same point, and at the junction of the basi-occipital and ex-occipital bones, the posterior Eustachian passage is dilated into the rhomboidal sinus, from which it is continued by a short and open canal into the posterior, internal and inferior angle of the tympanic cavity. The anterior communicating canal passes forward into the basi-sphenoid, where it divides into a pair of anterior Eustachian passages. Each of these is dilated and again contracted within the basi-sphenoid, traverses the pro-otic for a short distance, and finally enters the tympanic cavity adjacent to the cochlea, and immediately in advance of the foramen of exit for the internal carotid artery.

The Eustachian passages, together with the tympanic cavity and the external auditory meatus, represent the cleft between the mandibular and hyoidean arches, and constitute the only post-oral communication between the pharynx and the external medium which persists in the adult crocodilian skull.[1]

In the fresh subject the median and two lateral canals are continued downwards through the soft parts as membranous tubes, until they converge at an inferior valvular orifice upon the surface of the palate. Professor Owen has suggested that the Crocodilia, which habitually float with the ears submerged, may possibly maintain an auditory communication with the air by means of these Eustachian passages; for they open, as also

[1] "The tympanic cavities of embryonic crocodiles communicate with the mouth by wide and simple apertures; and the complicated arrangement of canals just described results from the great downward development of the basi-sphenoid and basi-occipital, and their encroachment upon these apertures on the inner side, while the quadrate bone narrows them on the outer."—Huxley, *Anat. Vert.* p. 256.

do the long nasal passages, into the pharynx, which can be shut off from the mouth by the velum palati.[1]

The following canals and passages open into the tympanic cavity :—

External Wall.—The meatus auditorius externus.

Internal Wall.—The fenestra ovalis and the meatus auditorius internus, the anterior and posterior Eustachian passages, the anterior part of the carotid canal, and the communication above the brain-case with the tympanic cavity of the other side.

Posterior Wall.—Foramen for facial nerve, &c., beneath the meatus auditorius externus, passage for vein which joins the jugular vein, posterior part of the carotid canal, and immediately within the tympanum the canal (*foramen aërosum*), which traverses the quadrate and communicates with the air-spaces of the mandible.

Anterior Wall.—Foramen beneath the fore part of the meatus auditorius externus; canal in pro-otic, which emerges in the pterygoid fossa, dividing into two below; and passage of exit of the temporal artery, leading into the supra-temporal foramen.

The bony framework of the internal ear is furnished entirely by the periotic bones. It consists of the vestibule, the cochlea, and the semicircular canals. The inner wall of the bony vestibular chamber forms that pyramidal projection seen from the cerebral cavity; it is formed mainly by the pro-otic and opisthotic bones, but is completed above by the epiotic. The fenestra ovalis opens outwards from its lower part, and is bounded, as is always the case when the periotic bones are distinguishable, by the pro-otic and opisthotic in nearly equal proportions. The cochlea lies in a nearly vertical position, beneath the vestibule; its apex, which is directed downwards, resting in a pit excavated at the junction of the basi-occipital and basi-sphenoid. The anterior wall of the cochlear cavity is formed by the pro-otic, and its posterior wall by the opisthotic, while externally it is partly supported by the cochlear loop,[2] a process of the opisthotic,

[1] Owen, "On the Communications between the Cavity of the Tympanum and the Palate in the Crocodilia," *Phil. Trans.* 1850, Part II.

[2] "Petrosal" of Owen, "*Laqueus Owenii*" (satirical, surely) of Brühl.

which curves round to join that part of the pro-otic which forms the anterior wall of the cochlea. The semicircular canals lie in the thick mass of bone which forms the upper and outer walls of the vestibule. They are three in number; an anterior, excavated in the epiotic and pro-otic bones; a posterior, in the epiotic and opisthotic, and an external, in the pro-otic and opisthotic.

The periotic bones are bounded anteriorly by the alisphenoid, posteriorly by the ex-occipital (blended with the opisthotic), superiorly by the supra-occipital (blended with the epiotic), inferiorly by the basi-sphenoid (pro-otic) and basi-occipital (opisthotic), internally by the cranial cavity, and externally by the quadrate.[1]

In the majority of Sauropsida the QUADRATE is more or less movable, but in Crocodilia, Chelonia, and *Hatteria*, it is firmly wedged in among the cranial bones, and furnishes a rigid pivot for the lower jaw. In Ophidia alone does the quadrate abut upon the squamosal. In Crocodilia it occupies its normal position, in relation with the periotic bones by one end, and with the articular piece of the mandible by the other.

The quadrate is prismatic in shape. It presents a superior surface, part of which forms the floor of the lateral temporal fossa; a posterior surface, blended with the first towards the articular extremity of the bone, and largely occupied by the articulation with the ex-occipital; and an inferior surface, which forms a great part of the pterygoid fossa. We may further distinguish, for purposes of description, the condyle, and the extremely irregular anterior end.

A large proportion of the superior surface is occupied by jagged articulations. Its external margin is overlapped by the quadrato-jugal for about four-fifths of its extent, the post-frontal resting upon the anterior fifth.[2] The squamosal is attached to the internal margin, and again to a small space internal to the post-frontal. The middle of the surface is smooth and non-articular. In front it is marked by a semilunar depression, which forms part of the external auditory meatus; behind this

[1] It will be seen that this account of the periotic bones owes much to Professor Huxley's *Elements of Comparative Anatomy*.

[2] This is the usual arrangement; but sometimes the squamosal descends so as to exclude the post-frontal.

is an elongated space which helps to bound the lateral temporal fossa.

Posteriorly, the quadrate articulates with the ex-occipital by a large, rough surface, divided diagonally by a groove. This groove, formed into a canal by the adjacent bone, transmits the facial nerve, and some vessels. That part of the quadrate which bounds the tympanic cavity is also seen upon this surface; it has already been described in detail. Upon the posterior wall of the cavity a canal is seen to enter the quadrate: it may be traced by a bristle to an elongated aperture situate on the smooth part of the posterior surface near the condyle. In some skulls this canal is divided into two for a greater or less extent. Stannius[1] first pointed out that by means of this canal a pneumatic communication subsists between the tympanic cavity and the articular piece of the mandible. In fresh specimens it is lined by a continuation of the mucous membrane of the tympanum.

The inferior surface looks into the pterygoid fossa; it is quite smooth, and the mandibular muscles play against it. This surface is continued upwards and forwards into a saddle-shaped concavity, which forms part of the posterior wall of the supra-temporal fossa.

The saddle-shaped concavity just mentioned forms the upper third of the anterior or internal edge of the quadrate. Immediately below it is an extremely irregular and jagged surface, terminating below in a pointed triquetrous projection. The anterior margin of the upper part of this articular surface gives attachment to the alisphenoid, the adjacent posterior part to the pro-otic, while the inferior projection is wedged in between the basi-sphenoid internally and the pterygoid externally.

The articular end of the quadrate, seen from behind, has somewhat the figure of an hour-glass. The external dilatation is the larger and more protuberant, the internal being flattish. A slight concavity (which also enters into the joint) intervenes. The posterior tip of the adjacent quadrato-jugal forms part of the condylar surface, and like the articular end of the quadrate, exhibits numerous small pores, such as indicate the place of attachment of a fibro-cartilage.

[1] *Zootomie der Amphibien*, p. 164.

The quadrate articulates with nine bones, viz., the ex-occipital, basi-sphenoid, alisphenoid, pro-otic, quadrato-jugal, pterygoid, post-frontal, squamosal, and articular piece of the mandible.

Like the frontals and parietals, in the crocodilian skull, the PTERYGOIDS are united by ankylosis during fœtal life, and cannot be afterwards separated without fracture. Thus united, they consist essentially of a median part, which envelopes the posterior portion of the nasal passages, and two expanded horizontal plates, whose upper side looks into the pterygoid fossa, while the under side forms the posterior part of the bony palate.

For purposes of description the pterygoids may be divided into the superior nasal process, the inferior nasal process, the nasal septum, the ascending process, the crest, the lateral plate, and the external margin.

The superior and inferior nasal processes form respectively the roof and the floor of the nasal passages. As seen in the united pterygoids, they resemble a double-barrelled gun.[1] The space between the two barrels is filled up in its posterior half by the crest, while the lower half of both barrels is furnished in the anterior half, not by the pterygoids, but by the palatals. The bony nasal septum arises by the confluence of the superior nasal processes of both sides. It divides the two tubes more or less completely, according to the age and species of the specimens examined. When fully formed, its lower edge rests upon the inferior nasal process behind, and upon the palatals in front. In adult skulls, it is conspicuous from without, as dividing the posterior nasal aperture. Anterior to the pterygoids, the nasal passages are divided by the vomer, the horizontal plate replacing the superior nasal process, while the perpendicular plate continues the nasal septum. In birds, Ophidia, and most Lacertilia the posterior nares are bounded by the palatals, and divided by the vomer.[2] In Crocodilia, on the other hand, they are produced backwards so far as to be bounded by the pterygoids, and divided by the pterygoid septum. This backward extension of the nasal sacs is doubtless connected, as examination of the soft

[1] This part of the nasal tract is, in some crocodiles, greatly expanded laterally, so as to give rise to nasal bullæ, which project into the pterygoid fossa.

[2] Huxley, *Elements of Comparative Anatomy*, p. 232.

parts shows, with the peculiar faculty which the *Crocodilia* possess of biting under water without admitting water to the pharynx.

In all tertiary and post-tertiary crocodiles this special modification is found, but not in those of earlier geological age. It is very interesting to find the earliest known Crocodilians less specialised and more lacertilian in this respect than those of later date. The triassic genera *Belodon* and *Stagonolepis* have the posterior nasal apertures far forward, and not surrounded by either palatals or pterygoids. In the post-triassic secondary crocodiles (*Steneosaurus*, *Teleosaurus*, &c.), the posterior nares open in the palatals, but the pterygoids are not in contact with them. Lastly, in the post-cretaceous species both palatals and pterygoids give off bony plates which surround the nasal passages, and the posterior nares open in the pterygoids. A similar progressive modification is observed, *pari passu* with geological time, in the Eustachian passages. The triassic species have no bony canals for these communications; in the later secondary Crocodiles the middle Eustachian canal is inclosed by bone, while the highly complex system of median and lateral bony Eustachian passages exists only in the tertiary and recent forms.[1]

It should be remarked that the closing in of the palatals and pterygoids upon the nasal passages belongs to a comparatively late stage of development (see Appendix, p. 49).

The inferior nasal processes bound the posterior nares below.[2] The suture between them is persistent; nowhere else in the adult skull are the two pterygoids separable.

The posterior nasal apertures vary somewhat in position and aspect. In the *Alligatoridæ* they look downwards, in the Crocodiles and Gavials backwards as well as downwards. When, as in the adult *Alligator Mississippiensis*, the aperture opens altogether upon the palatal surface, the pterygoids may present an unbroken occipital surface of moderate extent.

The external sides of the ascending processes are smooth, and look into the pterygoid fossa. The internal surfaces are exceed-

[1] Huxley, *Q. J. Geol. Soc.* vol. xxxi., pp. 423-438 (1875).

[2] In *Alligator Mississippiensis* the cavity is at this point dilated internally and divided by bony septa.

ingly jagged: they articulate with the basi-sphenoid, which fits into the notch between them, and bound for a small extent the rhomboidal (Eustachian) sinus. The upper margin of the ascending process articulates with the quadrate, and, by a small part of its anterior border, with the alisphenoid.

The crest of the pterygoids occupies the middle line upon the upper surface for about two-fifths of the longitudinal extent of the bone. It rises gradually from between the two convex superior nasal processes, and attains its greatest height at the level of the anterior edges of the ascending processes. In front, the crest supports the cartilaginous interorbital septum; behind, it articulates with the under surface of the basi-sphenoid.

The lateral masses of the pterygoids are greatly expanded. Their upper surface looks into the pterygoid fossa, and lodges the mandibular muscles; the lower forms the posterior part of the bony palate; the posterior edge is smooth, and gives attachment to the external pterygoid muscle. The external margin is thickened and considerably raised. When covered with the soft parts this edge is in contact with the inner surface of the mandible. The anterior margin is chiefly articular. The palatals are attached from the middle line outwards for a distance equal to about one-third of the greatest breadth of the bone. A small smooth indentation lies adjacent to the pterygo-palatine suture, and constitutes the posterior boundary of the palatine foramen. External to this the transpalatine is attached to the remainder of the anterior margin of the pterygoid, as well as to a considerable part of the external border of the same bone.

Each pterygoid articulates with seven bones, viz., the palatal, pre-frontal, transpalatine, basi-sphenoid, quadrate, alisphenoid, and fellow pterygoid.

The TRANSPALATINE (*os transverse* of Cuvier) connects the pterygoid with the jugal and maxilla. It consists of a central flattened bar of bone, from which three processes are given off. The axes of these processes are nearly in the position with respect to each other of the three axes of a regular solid; two of them are curvilinear. We have a pterygoid process, passing downwards and somewhat backwards to articulate with the external, and partly with the anterior margin of the pterygoid; a maxillary process, which passes forwards close to the alveolus

of the hinder teeth; and a jugal process, which is directed upwards and inwards, lying with its external surface in contact with the jugal, while it touches the post-frontal with the superior extremity. The anterior margin of the transpalatine forms about two-fifths of the external boundary of the palatine foramen; the posterior margin is placed vertically, and directed towards the pterygoid fossa. The transpalatine has two expanded smooth surfaces, an outer and an inner; the first is covered by the mucous membrane of the mouth; the other is in contact with the mandibular muscles which fill the pterygoid fossa.

The PALATALS may occupy about one-third of the length of the palate, and lie immediately in advance of the pterygoids. Besides forming a considerable part of the roof of the mouth, their superior surfaces constitute the floor of the nasal passages along the whole course of the bones. Each presents for examination an inferior surface, a superior surface, divided into two by a prominent longitudinal ridge, an external border, anterior, posterior and internal articular edges, and an ascending articular process.

The inferior surface is smooth, and forms part of the bony palate. One or two vascular foramina are visible upon it. The superior surface is divided into two parts by a longitudinal ridge, which is comparatively low behind, rises into the conspicuous ascending process at the junction of the posterior and middle thirds of the bone, and in the anterior two-thirds forms the elevated margin of the external half of the bone, which is here raised above the level of the adjacent floor of the nasal passage. The external portion of the superior surface adjoins the palatine foramen. In *Alligatoridæ*, this part of the surface is deeply excavated by cells of considerable extent. Behind the ascending process, the longitudinal ridge is low, and serves mainly for attachment of that tubular prolongation of the pterygoid which here bounds the nasal passage laterally as well as above. In front of the ascending process, the longitudinal ridge, supported on its outer side by a bony mass, rises much higher and closes in the side of the nasal passage, the superior nasal process of the pterygoid furnishing little more than the roof of the meatus. The horizontal plate of the vomer is in contact with the internal edge of the ridge for some distance

(varying according to the species) towards the front of the palatal bone. The ascending process of the palatal is strengthened by a similar and contiguous process given off from the pterygoid. It rises considerably above the general level of the superior surface, and articulates (as is very commonly the case in other animals) with the descending process of the pre-frontal. The external margin of the palatal is concave and smooth; it forms the internal boundary of the palatine foramen. The anterior edge of the bone articulates with the maxilla; the suture extends furthest forwards at the middle line, and thence passes backwards in a rapidly retreating curve. The edge itself is deeply grooved and receives a corresponding projecting bevel of the maxillary bone. Behind, a jagged and irregular suture connects the palatal with the pterygoid. In the majority of Crocodilia, the two palatals are in contact by their inner edges for the whole length of the bone, and upon the suture rest the nasal septum of the pterygoid and, for a short space in front, the bases of the vomers. In *Tomistoma*, however, the palatals diverge a little anteriorly, and the expanded bases of the vomers appear on the palate.

In all, the palatal articulates with five bones, viz., the pterygoid, pre-frontal, vomer, maxilla, and fellow-palatal.

The VOMERS of Crocodilia are paired bones,[1] which continue forwards the superior nasal processes of the pterygoids, and in a similar way divide and partly cover in the nasal passages. They are delicate bones, and in parts translucent. Each vomer consists of a perpendicular plate, a horizontal plate, and a base. The external wall of the perpendicular plate bounds the nasal passage of the same side; while internally the perpendicular plates of the two vomers diverge, and prolong the groove formed on the superior surface of the pterygoids. The horizontal plate is triangular, much produced longitudinally, and having its obtuse angle external. It roofs in the posterior nasal passage, which communicates with the proper nasal cavity immediately in front of the short anterior side of the triangle. In a fresh skull the posterior passage is seen to begin at this point by descending obliquely backwards on each side of the nasal

[1] The vomer is single in most fishes; double in Ganoids, Batrachia, Lacertilia, Crocodilia, and Ophidia; single in Chelonia.

septum. The posterior border of this triangle is applied to the ongitudinal ridge of the palatal in advance of the ascending process, while the posterior angle is overlapped by the extremity of the superior nasal process of the pterygoid. In front, the horizontal plate descends somewhat upon the side of the perpendicular plate, so as to be overtopped internally by a thin crest of bone which curves inwards. The base of the vomer rests with the posterior and larger part upon the median interpalatal suture; but for a short distance upon the median maxillary suture. In *Tomistoma* the bases of the vomers appear in the palate, and together present the form of a much elongated lozenge, the posterior converging sides being bounded by the palatals, and the anterior by the maxillæ, while in *Jacare* they are visible between the pre-maxillæ and maxillæ. The two vomers articulate with each other by their bases, the one overlapping the other to a small extent.

The vomer articulates with four bones, viz., pterygoid, palatal, maxilla, and fellow vomer.

The MAXILLA forms the roof of the mouth forwards from the anterior boundary of the palatine foramen to near the extremity of the snout, a relatively small share in front being contributed by the premaxilla. It largely bounds the nasal passages in the anterior part of their extent, and appears also in the face and within the pre-orbital cavity. Further, it supplies the greater part of the dental alveolus, only a few of the very foremost teeth being lodged in the premaxilla. We have therefore principally to consider the superior or facial surface of the bone, the internal or nasal surface, the inferior or palatal surface, and the external margin or alveolus.

Like all the facial bones, the maxilla has an irregular and deeply-pitted tegumentary surface. The sculpturing is due to the attachment of the skin, while the numerous foramina are the openings of nervous and vascular canals. The superior surface of the maxilla is bounded in front by the premaxilla, internally by the nasal, and posteriorly by the pre-frontal, lachrymal, and jugal.

The internal or nasal surface is deeply concave. In front it forms the external and lower walls of the bony nasal passage, behind it recedes outwards, and helps to inclose the cavity in

which the lateral nasal sacs lie. The apertures of several sinuses are seen upon this aspect. Upon the orbital surface is a vascular foramen. Adjacent to the anterior edge of the palatine foramen are two large and irregular openings which look backwards. The internal and larger of these lodges an extension of the nasal sacs; the external and smaller leads into a canal, the alveolar sinus, which traverses the maxilla, enters the premaxilla, and transmits the superior maxillary nerve and vessels. The anterior part of the nasal surface is also excavated by a vascular canal directed backwards, and opening into the alveolar sinus.

The palatal surface is flat and smooth. It is bounded behind by the large foramen and the palatal bones, internally by the other maxilla, and in front by the premaxilla. Externally it terminates in the dental alveolus. The palatal surface adjacent to the alveolar border is marked by many vascular canals; the more conspicuous of these may readily be traced by a bristle, when they will be found to proceed from the alveolar sinus, and to communicate with the foramina opening into the preorbital space.

The teeth of Crocodilia are restricted to the maxilla, premaxilla, and mandible. At first the maxillary alveolus is a simple groove, which becomes gradually converted into a series of sockets by the growth of transverse bars of bone.[1] The sockets are first completed in the anterior region of both jaws, so that young skulls shew a dental groove undivided behind. On the inner side of the alveolus pits are seen, which receive the tips of certain of the mandibular teeth. The position, number and depth of these pits vary according to the species. In *Gavialis* they are wanting altogether, and in *Tomistoma* they lie between the teeth.

The tabular mass of bone, which constitutes the palatal process, is connected with the rest of the maxilla along its external border, and further by a vertical buttress which divides the

[1] In the extinct Plesiosauria and Dinosauria the teeth are similarly implanted in sockets; in Ichthyosauria they are lodged in a continuous groove. Ophidia have the teeth ankylosed to the jaw; Chelonia are edentulous; Lacertilia exhibit several different modes of implantation, but they never have distinct teeth in separate sockets, except perhaps in the extinct *Proterosaurus*.

longitudinal nasal passage from a double canal on its outer side. A cross section of the maxilla and nasal, made at or near the so-called canine tooth, resembles a letter A laid on its side. The palatal process and the facial plate represent the converging lines; the cross-piece is the vertical buttress or septum. The external or triangular space is traversed by the superior maxillary nerve and vessels; an extension of the nasal sacs lies below and internal to it; while the internal space (quadrilateral in section) contains the longitudinal nasal passages, divided from one another in the fresh skull by the internasal septum.

The palatal process extends inwards so far as to be in contact with its fellow for the greater part of its length, and throughout this extent it forms the floor of the nasal passage. Where the two join, a ridge is developed, to the fore part of which the inter-nasal cartilage is attached, while the posterior part of the suture supports the anterior portion of the base of the vomer.

The PREMAXILLA is the continuation of the maxilla forward to the end of the snout. Like the maxilla, it has its alveolus, palatal process, and nasal passages, and the structure of these parts is similar in the two bones.

The alveolus receives the four or five front teeth on either side.[1] The pits for the mandibular teeth are placed as in the maxilla. The first pair, which receive the two anterior mandibular teeth, are particularly large, and are often converted into perforations (bitten through, as it were) in adult skulls. In the *Alligatoridæ* the fourth mandibular tooth bites into a similar pit, but in other Crocodilia it is received into a lateral notch (the canine groove) at the premaxillo-maxillary suture. The upper jaw is in all cases more or less constricted at this point, though very slightly in *Alligator Mississippiensis*.

The nasal passages terminate in the premaxillæ at the anterior nasal aperture, which appears on the upper side of the skull as a roundish or oval median space, divided more or less perfectly in some species by the produced nasal bones. Immediately beneath the nasal aperture the palatal plate is pierced by a smaller opening (the premaxillary aperture[2]), which may be

[1] In *Tomistoma* alone are there normally four pre-maxillary sockets.

[2] *Foramen incisivum* of authors.

roundish, heart-shaped, or sagittate. This inferior aperture is only seen in the dry skull; in the living animal it is closed by the mucous membrane of the mouth.

The premaxilla articulates with the maxilla by a transverse suture, whose direction varies much in different species. The palatal plates of opposite sides are united, and the premaxillæ are always in contact in front of the nasal aperture. Behind the aperture, the premaxillæ may be adjacent for some distance (as in *Crocodilus intermedius*), or the nasal bones may be interpolated, so as to reach, and in some cases to divide, the external nostril.

The NASALS are two long splints which extend along the face, one on each side of the middle line and adjacent to it, from the frontal to, or near to, the anterior nasal aperture. During the greater part of this extent they are bounded on the outer side by the maxillæ, but in front they touch and partly separate the premaxillæ, while they are externally in contact with the prefrontal for a greater or less distance behind. Specific distinctions are founded on the forward extension of the nasals. In some Crocodilia (e.g. *Alligator Mississippiensis*) they divide the anterior nasal aperture completely; in others (*Crocodilus vulgaris*, &c.) they reach the aperture, but do not extend across it; while in *Crocodilus intermedius*, *C. cataphractus*, and the *Gavialidæ*, they do not reach the aperture at all. The underside of the nasal bone forms part of the roof of the nasal passage, and is grooved for the olfactory nerve.

The FRONTALS are originally distinct bones, and, in an early stage of embryonic life, are separated from each other by a considerable interval. By the time the crocodile leaves the egg they are united into one bone, and no trace of the suture is apparent in the adult skull. In front, the united frontal is overlapped by the nasal bones in the middle, and by the prefrontal on either side; behind, it is articulated by a jagged suture to the parietal and the two post-frontals. It forms nearly a third of the inner border of the orbit, and generally rises into a ridge along the upper orbital margin. The non-articular part of the superior surface is subcutaneous and deeply pitted. Laterally, the frontal presents no important feature, except the inner wall of the orbit, which is concave

in both directions. The inferior surface in its posterior part roofs in the cerebral cavity for a short distance; and the alisphenoids, which form the anterior wall of the brain-case, are rather loosely attached to the two ridges which divide the cerebral from the orbital surfaces of the frontal. These ridges converge forwards, and between the orbits they bound the olfactory groove, which is here very strongly defined.

Cuvier succeeded in tracing a real or supposed correspondence between all the bones of the crocodilian skull and certain elements of the skulls of mammalia, with two exceptions. He was able to find no homologues among the mammalian facial bones of two membrane-bones adjacent to the frontal, which are present in Crocodilia, as well as in other lower vertebrates. These bones from their position he denominated the anterior and posterior frontal, names which, together with the synonymous terms, pre-frontal and post-frontal, are still in use. The names must not be held to imply correspondence of the three frontals of the crocodile with the frontals of mammalia,[1] but merely to remind us that all three are contiguous, and that their relative position is constant.

The PRE-FRONTAL lies external to the frontal, and partly in advance of it. It overlaps the posterior edge of the nasal, and part of the nasal process of the frontal. Its external edge contributes about one-third of the inner wall of the orbit, and through the remainder of its extent is conterminous with the lachrymal. The superior or facial surface presents no features of special interest. Like the other bones of the face, it is pitted; the orbital margin is raised or nearly flat, according to the species. The inferior surface looks partly into the orbit and partly into that pre-orbital space which lodges the nasal sacs. From the angle between these two a descending process is given off, which articulates by its inferior extremity with the pterygoid and palatal bones, as previously described (p. 28). Each descending process sends inwards a lateral projection, which articulates with the same part of the fellow bone, thus forming a short horizontal shelf upon which the free ends of the olfactory bulbs rest.

[1] The pre-frontal corresponds with the lateral mass of the ethmoid, while the post-frontals are unknown in the mammalian skull.

The POST-FRONTAL occupies the anterior and external angle of the quadrangular cranial roof. Its internal and concave edge helps to circumscribe the supra-temporal fossa. The connections of the post-frontal, which forms an important buttress of the cranium, are numerous. Internally it articulates with the frontal and the parietal, posteriorly with the squamosal. A concavity upon its inferior surface receives the superior articular head of the strong ridge upon the alisphenoid (p. 15); from near this point a small process passes outwards and backwards to join a prolongation of the quadrato-jugal. There is further a descending process of the post-frontal, which in the dry skull appears to divide the orbit into two parts, but which in reality separates the orbit from the lateral temporal fossæ; this descending process meets a similar projection from the jugal, and also sends down a long and thin prolongation which reaches the transpalatine.

The PARIETAL is a membrane bone, originally double, but early united into a single piece. It forms the median and posterior element of the quadrangular cranial plate, and may extend backwards to its very edge, though a membrane-bone united with the supra-occipital (dermo-supra-occipital) usually succeeds it on the roof the skull. The inferior surface of the parietal helps to inclose the brain-case, adjoining the supra-occipital and periotic bones behind, the frontal anteriorly, and the alisphenoid on either side. The parietal and frontal contribute nearly equal shares to the roof of the cerebral cavity, just as the basi-occipital and basi-sphenoid do to its floor. The hinder part of the inferior surface exhibits a number of air-cells, which communicate laterally with each other, as well as with the tympanic cavities of the supra-occipital and epiotic. The boundaries of the bone are not always easily determined in this direction, as it usually forms an intimate union with the adjacent bones, particularly with the epiotic and supra-occipital.

Externally the parietal is articulated with the squamosal and post-frontal, the two attachments being separated by the supra-temporal fossa, whose entire internal border is furnished by the parietal. The supra-temporal fossa opens behind into a small cavity or canal (much contracted in the adult skull) which leads to the occipital surface. Its roof is commonly formed by the

squamosal and parietal jointly, and through it the temporal artery enters the skull. Anteriorly the parietal articulates with the frontal by means of a jagged suture.

Each half of the parietal articulates with seven bones, viz., frontal, alisphenoid, post-frontal, pro-otic, squamosal, epiotic, and supra-occipital.

The LACHRYMAL bone occupies the anterior angle of the orbit, and passes forwards upon the face for a short distance. It lies between the pre-frontal and the jugal, and is bounded in front by the maxilla, in some cases by the nasal also. The superior or facial surface is in certain species, particularly in *Crocodilus biporcatus*, marked by strong raised lines or ridges. Near the inner side of the orbital edge a round foramen is seen, which expands within the bone into a large flattened cavity. The naso-lachrymal sac is here lodged; it receives the outflow from the lachrymal ducts, yielding also a peculiar secretion of its own, and empties itself into the nasal passages anterior to the lateral sacs. Upon the inferior surface of the bone, and near its anterior extremity, the laterally elongate aperture appears, by means of which the internal cavity of the bone opens into the lachrymal fossa.

The lachrymal primitively belongs to the membrane-bones of the orbital ring. Its appropriation to the reception of the lachrymal duct gives constancy and a definite position to this ossification alone out of the highly variable group to which it belongs; it is commonly present in vertebrates higher than fishes.

A loose SUPRA-ORBITAL bone lies in the eyelid adjacent to the junction of the frontal and pre-frontal, on the inner wall of the orbit.

The JUGAL bone occupies the posterior part of the side of the face. It has the maxilla in front, and the quadrato-jugal behind; internally it adjoins, in order from before backwards, the lachrymal, the orbit, the post-frontal, the lateral temporal space, and the quadrato-jugal. The buttress-like transpalatine supports it beneath. In shape the jugal is long and flattened, broader at the maxillary end than behind. From near the middle of the inner surface a spur is given off, which meets a similar process of the post-frontal, forming thus a bar of bone, which divides the orbit from the open space which occupies the anterior

portion of the lateral temporal fossa. The external border of this space, and also that of the orbit, are furnished almost exclusively by the jugal.

The QUADRATO-JUGAL lies wedged in between the jugal and the quadrate, its long diameter being oblique to the axis of the skull. The anterior concave edge of the bone bounds the lateral temporal space. The inferior surface, which is smooth and very narrow, looks into the pterygoid fossa; the superior surface is partly rough and subcutaneous, but a long slip, which runs inwards and forwards to meet the post-frontal, and in some cases a large part of the inner border also, are smooth, and help to form the floor of the lateral temporal fossa.

The quadrato-jugal articulates with three bones only, viz., the jugal, quadrate, and post-frontal.

The SQUAMOSAL forms the external and posterior angle of the quadrangular cranial plate. It roofs in the meatus auditorius externus, part of the lateral temporal fossa, and more or less of the small posterior aperture through which the temporal artery enters the skull (p. 35), while it bounds the supra-temporal fossa for about one-fourth of its circumference. Its relations are with the ex-occipital and supra-occipital behind, the quadrate both before and behind the meatus auditorius, the post-frontal anteriorly, and the parietal internally. The superior surface is rough and pitted; the inferior smooth, except where other bones are articulated. A descending plate is given off from the squamosal close to the posterior edge of the bone. This plate varies greatly in depth in different species. It may descend so low as to expose a considerable occipital surface, and to form at the same time much of the posterior wall of the lateral temporal fossa. The quadrate is articulated to its anterior, the ex-occipital to its posterior side.

The INTER-ORBITAL SEPTUM rises in the middle line of the skull upon the coalesced trabeculæ cranii, and separates the roof of the mouth from the anterior cerebral vesicle. In the adult it underlies the optic, and further forward, the olfactory nerves. Its anterior extension constitutes the inter-nasal septum.

A small part of the inter-orbital septum is ossified in Crocodiles, forming the rostrum of the basi-sphenoid. No ethmoid or turbinal bones are present.

Lateral plates are given off from the top and bottom of the inter-orbital and inter-nasal septum, and these form a complicated system of nasal passages, extending between the external nostrils and the orbit, and communicating through the palatals and pterygoids with the posterior nares. The superior lateral plates form the roof of the nasal sacs, and represent the lateral cartilages of the nose in mammalia. They are invested by the nasal and lachrymal bones above, and laterally by the maxillæ and premaxillæ. Immediately in front of the eye, the walls of the nasal chamber are excavated by lateral sacs, of which there are two on each side of the head. The inferior cartilaginous plates extend from the external nares to the palatine arches, which lodge the posterior nasal passages; an interval occupied by membrane alone passes obliquely downwards and backwards along their external edges and separates them from the superior plates.

Of the lateral nasal sacs the posterior are much the larger. They occupy the front of the orbit between the pre-frontal, lachrymal, nasal, and palatal bones, and come nearly in contact with the eyeball. Internally, they project into the longitudinal nasal passages, communicating therewith by a small round aperture. The anterior lateral sacs lie close to the fore-end of the palatine foramina and open into the longitudinal nasal passages by a pair of oval foramina.

There is further an external appendage of the nasal passages, which lies outside and in front of the posterior lateral sac. It is contained in the pre-orbital cavity, extending forwards into the inner of the two tubes which excavate the external angle of the maxilla, and communicates with the longitudinal nasal passage by an aperture intervening between the edges of the superior and inferior plates.

The lachrymal sacs partly overlie the anterior lateral sacs, and enter the longitudinal nasal passages immediately in front of them. The posterior nasal passage of each side descends obliquely backwards beneath the fore edge of the horizontal plate of the vomer, and enters the palato-pterygoid tube, along which it passes to the back of the skull.

An inter-orbital septum is developed in most fishes, not in any Amphibia; it is found, except in Ophidia, in all reptiles

and birds; it is the mesethmoid (osseous or cartilaginous) of mammals.

Each side of the lower jaw or MANDIBLE of the Crocodile consists of six pieces. These are

1. Dentary.
2. Angular.
3. Surangular.
4. Splenial (Opercular[1].)
5. Coronoid[2] (Complementary.[1])
6. Articular.[3]

The articular, coronoid and splenial are restricted to the internal aspect of the mandible; the other three appear on both surfaces.

The dental alveolus is furnished by the dentary bone alone, though the splenial strengthens its inner border for a greater or less distance behind, while the surangular overlaps its posterior end. In structure the alveolus resembles that of the maxilla, but the large teeth ("canines") alternate with the maxillary canines, and the large teeth of one jaw are consequently opposed to weak and relatively undeveloped teeth in the other. The sockets for the teeth are comparatively distant in front, and often confluent behind.

A large part of the external surface of the mandible, including the dentary and part of the surangular portions, is subcutaneous, pitted, and pierced for vascular and nervous supply.

The mandibular symphysis varies accordingly to the proportions of the mouth. In the short-nosed Crocodilia (*Alligatoridæ* and *Crocodilidæ*) the dentary bones alone enter the symphysis. The rami are connected by a jagged suture, which perfectly resists backward and forward movement, but is loose enough to permit a slight lateral displacement of the rami. In the *Gavialidæ*, on the other hand, where the jaws are much produced, no lateral movement of this kind can be effected, for the dentary bones are rigidly interlocked, and the symphysis is strengthened behind by the splenials, which meet along the middle line,

[1] Terms adopted by Cuvier.

[2] In lizards this bone bears a coronoid process.

[3] Of these six pieces, the dentary, splenial and articular are most constant. The mammalian jaw is exceptional in being ossified in cartilage from two centres (one to each ramus).

and occupy the angle between the rami for a considerable distance.

Large openings exist in the hinder part of the lower jaw. On the outer side there is the external mandibular foramen, bounded by the dentary, angular and surangular pieces. Internally we find the internal mandibular foramen, lying between the angular and splenial. Both these foramina are closed by membranes in the fresh skull. The former gives passage to a cutaneous branch of the inferior dental nerve; the latter to branches of the inferior dental nerve and artery. The nerve to the mylo-hyoid may either pass out here or by a special foramen, which in some crocodiles pierces the splenial further forward. The mandibular fossa (which may be distinguished by this name from the mandibular foramina) opens backwards just in advance of the condyle. It lodges the mandibular muscles, and through it the inferior dental artery and nerve enter the mandible. The fossa contracts rapidly within the jaw, and ultimately divides into two parts, an alveolar canal, which lies in the dentary bone and communicates with most of the teeth, and an inner cavity in which the unossified prolongation of Meckel's cartilage lies. Branches of the inferior dental vessels and nerve are given off in *Alligator* through a foramen in the middle of the splenial. In *Crocodilus* the foramen is situated at the fore-end of the splenial, while in *Tomistoma* it lies in the symphysis.

The condyle is formed almost exclusively by the articular bone. Its principal surface is convex from side to side, and concave in the direction of the axis of the skull. Behind, the cavity is defined by a strong, slightly curved lateral ridge, and it is completed externally by the projecting edge of the surangular bone. Upon the inner side of the transverse ridge is a foramen (the *foramen aerosum*). It transmits air from the pneumatic canal, which traverses the quadrate, into the hollow cells which occupy the interior of the articular bone. This extension of the tympanic cavity into the mandible exists in all the families of Crocodilia, and probably in all the species. Behind the condyle the articular, angular, and surangular bones are united into a post-articular process, which projects backwards beyond the quadrate or any other part of the cranium. Here are attached the digastric and the external pterygoid muscles.

The external margin of the pterygoid plays against the internal surface of the splenial, and thus checks lateral movement of the mandible. The surface of both bones at this point is covered by a tough and glistening fibrous membrane.

The pieces which make up the mandible have the following situation and extent:—

Dentary. External surface from symphysis to external mandibular foramen. Internal surface:—a triangular space, having its base at the symphysis, and its apex at or near the hindmost enlargement of the alveolus. Includes also the whole alveolus and the alveolar canal, and is bounded by the fellow dentary, splenial, angular and surangular.

Angular. External surface:—the angle of the ramus, rising at most half-way up the side; forms nearly one half of the margin of the external mandibular foramen. Internal surface:—as far forwards as the internal mandibular foramen. Continued backwards along the whole of the under-side of the post-articular process. Bounded by all the other pieces of the same side.

Surangular. External surface:—the upper half of the ramus, posterior to the alveolus; forms the greater part of the upper margin of the external mandibular foramen. Internal surface:—upper and posterior part of the external wall of the mandibular fossa, external raised edge of the condyle; extends backwards a short distance upon the external and superior surface of the post-articular process. Bounded by all the other pieces of the same side.

Articular. Internal surface:—the condyle, and the greater part of the superior and internal sides of the post-articular process; part of the posterior wall of the mandibular fossa. Bounded by angular and surangular.

Coronoid. Internal surface:—a small space in front of the anterior edge of the mandibular fossa. Bounded by splenial, angular and surangular.

Splenial. Internal surface:—from the internal mandibular foramen and coronoid forwards to or near to the symphysis. Bounded by dentary, coronoid, angular and surangular.

The articular piece only is a cartilage-bone. It arises by the ossification of a part of the proximal end of Meckel's cartilage;

while the free end of the same cartilage becomes surrounded by five membrane-bones, which enlarge, unite, and complete the mandibular ramus.

The HYOID of the crocodile consists of a flattened shield-like body and two cornua. The body or basi-hyal is convex below, unossified, and marked along its fore-edge by three symmetrical pairs of notches, the second of which is considerably larger than the other two. On each side of the body of the hyoid and to a deep notch in the middle of its outer border, is articulated a cornu, which is tipped at both ends with cartilage, but otherwise fully ossified in the adult. The cornua pass at first backwards and upwards, but are bent at an angle about their middle point, and pass thence upwards and inwards.

It may be conjectured, though a more exact knowledge of the development of the crocodilian hyoid would be necessary to establish the point, that the cornua represent the branchial or thyro-hyal processes, and that the anterior (cerato-hyal) processes are either totally absent, or indicated only by the divisions (incompletely separated by the notches described above) of the anterior border of the body of the hyoid.

The hyoid has no attachment to the skull, but is connected with the windpipe by fibrous bands which pass on each side from the two projecting points of the emarginate posterior border of the basi-hyal. To the anterior part of the body of the hyoid is attached that vertical septum, which, when the hyoid is drawn forwards and upwards by the genio-hyoid and mylo-hyoid muscles, meets the velum palati and closes the pharynx.

"A minute styliform cartilage, which lies in close proximity with the *portio dura*, on the upper part of the posterior face of the quadrate bone, represents the *stylo-hyal*, or proximal end of the hyoidean arch." [1]

[1] Huxley, *Anat. Vert.* p. 256.

APPENDIX.

THE DEVELOPMENT OF THE SKULL OF THE CROCODILE.

[Translated, with Annotations, from *Untersuchungen über die Entwickelung und den Körperbau der Krokodile, von Heinrich Rathke, herausgegeben von Wilhelm von Wittich.* Braunschweig, 1866. Viertes Kapitel (Skelet). 1. (Schädel).]

In the embryo of the *Alligator lucius*,[1] the brain-case was still mainly cartilaginous and inclosed little more than the lower half of the brain, the upper half being for the most part covered only with integument and the proper brain-membranes. It consist d principally of an already chondrified portion of the investing mass (the so-called outer layer) of the notochord, and of the cartilaginous capsules for the membranous parts of the ear-labyrinths; and consequently of the posterior cerebral part of the so-called primordial skull. For although

[1] The embryos investigated by Rathke were the following :—

A. *Alligator lucius* (*Mississippiensis*). The body was much smaller than the yolk, in which it was half embedded. Length of head, 7 Paris lines; length of neck and trunk, 8 lines; length of tail, 11 lines; total length, 2 inches 2 lines.

B. *Alligator sclerops* (*Jacare nigra*)—Back part of the skull injured. Total length, 2½ inches.

C. *Crocodilus acutus* (*Americanus*)—Total length, 5½ in.

D. *Crocodilus acutus* (*Americanus*)—Total length, 6 in. 1 line.

E. *Alligator sclerops* (*Jacare nigra*)—Total length, 4 in. 1½ lines.

F. *Alligator cynocephalus* (*Jacare latirostris*)—Total length 6 in. 11 lines.

G. *Gavialis* (*Tomistoma*) *Schlegelii*—Total length, 11 in. 8 lines.

H. *Gavialis Tomistoma* (*Schlegelii*)—Total length, 12 in. 10 lines.

I. *Crocodilus acutus* (*Americanus*)—Total length, 10 in. 6 lines.

(Rathke, *Krokodile*, pp. 2—4.)

*** The Paris foot is 12·8 English inches.

the parietal and frontal bones were already discernible, they had attained but a very inconsiderable size. The facial bones could without difficulty be distinguished; they occupied the same relative positions as in the adult, but were in general very imperfectly developed as yet.

That part of the investing layer of the chorda dorsalis which in vertebrates generally is to be regarded as the foundation of the cranium, formed a plate of only moderate thickness, beneath that division of the brain which is posterior to the infundibulum, just as in other vertebrates whose notochord attains no corresponding thickness. This plate was somewhat longer than broad, and presented the form of an irregular oblong, rather narrower behind than in front. The finely pointed cephalic end of the notochord which lay inclosed in the substance of this plate did not extend quite to its middle point. Around it, the plate was of greater thickness, and took the form of a hollow cone with the apex directed forward. With the exception of the hinder end, which bordered on the occipital foramen, it was completely ossified. It enveloped the cephalic extremity of the chorda dorsalis as with a thin sheath, and was recognised as the body of the basi-occipital, which in young crocodiles has the form of a quadrangular plate, broader in front than behind. Before this was an elongated oval space, its long diameter lying in the axis of the cranium. Towards the oval space the plate was extremely thin, and, like the parts external and anterior to the oval space, cartilaginous. Close to its hinder end the basal plate gave off on either side a broadish flat process directed upwards, in the centre of which a nearly oblong speck of bone appeared, an indication of the ex-occipital, which in young crocodiles has, proportionally to its length, a very considerable breadth. Both processes were united over the prolonged spinal cord, to form an arch, whose median part was decidedly broader than the inferior or lateral parts. This median part was still altogether cartilaginous. In young crocodiles we find in its place not merely the ends of the ex-occipitals, much narrowed and nearly or quite in contact, but in addition the proportionally large, irregularly quadrilateral supra-occipital. The supra-occipital is thus formed in crocodiles, not in part only, as in many higher animals, but entirely, out of the investing mass of the notochord. Close behind its anterior end the tabular basis cranii, above described as still almost entirely cartilaginous and developed out of the investing mass of the notochord, sent upwards and rather forwards a short but relatively broad wing on either side. As yet these wings were entirely cartilaginous, subsequently they ossify and correspond to the posterior wings of the sphenoid in mammalia. The slight indication of the anterior wings

of the sphenoid which is present in young and adult crocodiles was equally small in the embryo.

The above-mentioned tabular part of the investing mass of the notochord passed anteriorly, as in other vertebrates higher than Batrachia, into those three processes which I have called "cranial trabeculæ" (Schädelbalken).[1] All three were entirely cartilaginous;[2] the middle trabecula was of inconsiderable length and moderate breadth; as usual, it was curved upwards and forwards, and lay in a transverse fold of dura mater. The two others extended forwards and rather downwards, so as to make an obtuse angle (the inferior aspect of the cranial flexure) with the basal plate, from which they proceeded. They converged somewhat rapidly at first, and then united together at some distance from their origin, so that in the interspace there remained a nearly triangular cavity of moderate vertical extent, which received the pituitary body together with the infundibulum. The opening of this cavity was closed by the mucous membrane of the mouth and by the tip of an involution of dura mater. As in many other vertebrates, which have passed through the earlier grades of development, these lateral trabeculæ give off, after their junction has taken place, a plate perpendicular to their own plane, of considerable length. The posterior half of this plate constituted a tolerably high inter-orbital septum, while the anterior half formed, on a lower level, the partition between the nasal sacs. The upper edge of the posterior half divided into two layers, which roofed in the orbits, while from the upper edge of the anterior half of the septum proceeded two lamellar, cartilaginous cornua in opposite directions. These processes, which I have termed the roofs of the nasal sacs (Nasendächer), sweep downwards round the upper and outer sides of the involutions formed by the olfactory membranes.

On the lower side of the middle trabecula, and in the foremost part of that cartilaginous basal plate which is developed out of the investing mass of the notochord, a small bony mass appeared, rather more than half as long as that which represented the basi-occipital, and like it, disposed lengthwise in the median plane of the body. This could

[1] Only two such processes are developed in Fishes and Batrachia.—*Author's Note.* The trabeculæ were described first in Rathke's Entwickelungsgeschichte der Natter, 1839. The "middle trabecula" is a transitory structure, occurring also in lizards, birds, and mammals, which represents a forward extension of the investing mass. In many lower vertebrates the lateral trabeculæ are primitively distinct from the investing mass.

[2] It may be questioned whether the middle trabecula had really undergone conversion into cartilage; the author probably means that none of the three was at all ossified.

be nothing else than the first trace of the body of the basi-sphenoid, since this, according to present knowledge of other animals, invariably takes its origin in the basal plate, immediately behind the space between that plate and the lateral trabeculæ, in which the pituitary body lies. On the other hand, there was as yet no trace whatever of the body of the pre-sphenoid.[1] In a young *Alligator sclerops*, which could only have survived its exit from the egg a short time, there might indeed be perceived the body of the pre-sphenoid. It was, however, still very imperfect, since it did not as yet extend forwards as a hatchet-shaped process with vertical sides, but consisted solely of a spatulate, horizontal bony plate, which formed together with the anterior part of the basi-sphenoid a cavity in which the pituitary body lay. This cavity is represented in young and adult crocodiles by the entrance to a canal which penetrates the base of the skull and opens on its lower surface.[2] A similar canal filled with cellular tissue may be discovered in certain mammalia and in man, but only for a short time after birth; commencing in the centre of the sella turcica, it terminates at some distance from the basi-occipital, and thus lies in its whole course between the pre-sphenoid and basi-sphenoid.[3] It must therefore seem strange that in young and old crocodiles this canal, taking an unexpected oblique course downwards and backwards, traverses the basi-sphenoid and emerges between that bone and the basi-occipital. This curious relation may be thus explained. The basi-sphenoid makes its appearance as a short piece, which in its further growth apparently sends downwards two separate, lamellar processes, one on either side of the cranium. These processes sweep round towards each other, and finally unite, forming thereby the anterior and inferior wall of the canal in question, and providing a surface of attachment for the pterygoids, which extend unusually far back. The hatchet-shaped process of the pre-sphenoid of the crocodile is developed in the cartilaginous inter-orbital septum, which arises by the coalescence to a great extent of the two lateral trabeculæ. The other, or posterior, half of the sphenoid is apparently developed out of those parts of the lateral trabeculæ which bound in front and on either side the originally simple vacuity of the base of

[1] Rostrum of the sphenoid, according to the preceding description of the skull.

[2] The upper part of this canal is ultimately appropriated by the pituitary body and carotid arteries, the lower part by the anterior communicating and median (Eustachian) canals.

[3] Vogt in his Inaugural-Dissertation has described with detail and exactness this canal as it occurs in mature human embryos and young children, and has also called attention to its significance.—*Author's Note.*

the cranium, since the entrance to the canal, into which this fontanelle is converted, lies between the pre-sphenoid and the basi-sphenoid. The alisphenoids, which in the embryo of *Alligator lucius* had only a relatively small length, must increase notably in the later stages of embryonic life, for in quite young crocodiles they are already of tolerable length. Orbito-sphenoids are not developed; they are, however, as Cuvier has pointed out,[1] represented by the alisphenoids, since in crocodiles several nerves emerge through the latter, which in higher animals pass out from the cranium between the orbito-sphenoids and alisphenoids.

The two tolerably thick-walled cartilaginous capsules destined to roof-in the membranous parts of the auditory labyrinths were of much greater size, relatively to the whole head and to the brain-case in particular, than the petrosals[2] of the adult crocodile, which they represent. These auditory capsules lay wedged in between the cartilaginous rudiments of the alisphenoids and ex-occipitals, overtopping these however, and in particular rising above the alisphenoids. In shape each somewhat resembled a hammer. That part which stood for the short and thick handle had its free extremity directed forwards; it presented the form of a bent cone rounded at the apex, and indicated the place of the cochlea. It was shorter in proportion to its thickness, as well as less curved, than the same part in young and adult crocodiles. The other half was somewhat thicker and altogether larger than the former, though the difference in thickness was less marked than at a later time; its axis was directed obliquely downwards and backwards. That surface of this latter portion which looked towards the brain-case was smooth and slightly concave. The external surface was considerably arched, and provided below with three slight and imperfectly defined protuberances, which correspond to the three semi-circular canals. Externally the capsules were slightly dilated for these semi-circular canals; but they appeared to have developed no processes internally between the canals to occupy the interspaces. On the external surface of the capsule there was, at the point where its two portions unite, a relatively large oval foramen,[3] of the same form as in the adult, and beneath this, separated from it by a short and delicate bridge of bone, a much smaller roundish or rather

[1] Recherches sur les ossemens fossiles, 4th ed. tom. ix. p. 153.—*Author's Note.* Stannius considers that the orbito-sphenoids are represented by two small ossifications which appear in the interorbital septum near the optic foramina (Supra, p. 15).

[2] Pro-otics of the foregoing description. The pro-otics represent, however, a part only of the ossifications of the auditory capsules.

[3] Fenestra ovalis.

elliptical foramen.[1] An operculum,[2] with an attached columella of the same form as in the adult, closed the oval foramen. No trace of a bony deposit could be detected even when the parts were dried; they were wholly cartilaginous.[3]

The proper frontals (principal frontals of Cuvier) consisted of two narrow and much curved bony slips, nowhere in contact, and wide apart behind. In the centre and in front a moderate interval existed between them, whereas in the young crocodile, when it leaves the egg, they not merely completely cover the fore-part of the brain, but are blended into a single plate. Each of these crescentic bones formed the upper boundary of the orbit of its own side. The concave border, which was directed downwards rather than outwards, was extremely thin, sharp, and tolerably firm. The internal or convex side was moderately thick, traversed in its whole length by a furrow, loose in texture, and pierced in many places so as to make a complicated network.

The parietals, which in young crocodiles, at the time when they quit the egg, are, like the frontals, anchylosed into a single plate, consisted likewise of two narrow slips of bone, which lay wide apart along their whole length, and were reticulated towards their upper and inner edges. They formed a pair of moderately curved plates situated above the cartilaginous auditory capsules, and touched the frontals anteriorly, whilst behind they extended as far as the arch of the future occipital segment. The widely separated position of both frontals and parietals was due, not merely to their slight breadth, but also to the circumstance that in the embryo the brain is proportionally much more voluminous than in the young or adult, and that on this account the membranous parts, which occupy the spaces between these bones and the still cartilaginous supra-occipital, are made to project as conspicuous eminences.

Where, on either side, the parietal and frontal came in contact, that ossification, which Cuvier calls the posterior frontal, was loosely attached. It extended downwards as far as the jugal; already it had a form similar to that of a much later stage of growth; at the same time its outstanding process was much thinner than in the adult or even in the young crocodile; moreover, it was not sub-cylindrical, but laterally compressed. Close behind this bone, and resting partly on the quadrate, was a very thin and almost horizontal plate, from whose

[1] Fenestra rotunda.

[2] Stapedial cartilage (stapes).

[3] For comparison with the above account consult the description which Windischmann has given of the petrous bone of the young crocodile in his treatise, "De penitiori auris in amphibiis structura." Lipsiæ, 1831.—*Author's Note.*

outer edge the external valve of the ear depends. This bone appears to me to be homologous with the tympanic bone of higher animals; others have called it the mastoid.[1] It was perfectly ossified, similar in form to that of the young crocodile, and was already of proportionately large size.

The quadrate had a form similar to that which it presents in young and adult individuals of *Alligator lucius*, but was in proportion to its length narrower and thinner in the lower half, which was already provided with a slight articular notch. It consisted essentially of a piece of cartilage, but in its middle third a very delicate bony crust surrounded the cartilaginous part as a short tube. By its broader and flatter upper half it was loosely attached to the outer wall of the cartilaginous auditory capsule, above and in front of the fenestra ovalis. Attached to that edge of the quadrate which was turned forwards and outwards, and in part overlying it, was a small lamina, elongated and pointed at both ends, whose axis was directed obliquely upwards and forwards. This lamina was thoroughly ossified. Cuvier has somewhat inappropriately identified this bone of the crocodile,[2] which is intruded between the quadrate and jugal, with the squamous portion of the temporal bone of mammalia.

With the quadrate a long, rather thin Meckel's cartilage articulated, and reached as far as the symphysis of the mandible. In the greater part of its length it was cylindrical and very gradually tapering forwards, but considerably dilated behind, where it joined the quadrate. Above the mandibular articulation it presented a hook-like process directed backwards, which however was of only small size, both absolutely and relatively. The thin and prolonged cylindrical portion was loosely inclosed by five very delicate but thoroughly ossified plates, which formed a sheath around it, leaving however between them greater or less intervals. Subsequently, these bony plates, as they became longer and broader, fitted completely into each other, and formed, as in Amphibia and birds, by far the greatest part of the ramus of the lower jaw. The above-mentioned dilated portion of Meckel's cartilage ossifies, and represents then the articular piece of the lower jaw (the angular bone of Cuvier).[3] In the embryo of the Gavial I found the articular bone for the most part ossified, while it was completely ossified in a very young *Alligator sclerops*.

The other bones of the skull were so fully ossified that neither at

[1] Squamosal of the foregoing description.

[2] Quadrato-jugal of the foregoing description.

[3] I am unable to find any passage in which Cuvier speaks of the articular bone as "angular."

their ends nor elsewhere could any particle of cartilage be detected which was not penetrated by bony matter. The jugals were tolerably thick and large plates, similar in shape to those of the young alligator. The lachrymals were also tolerably large, but differed from the form which they subsequently attain in this, that instead of a foramen for the passage of a lachrymal canal, there was only a groove, entering somewhat deeply into the expanded posterior end of the bone from below. The process[1] given off from the bones which lie between the lachrymals (the anterior frontals of Cuvier), did not, as it seemed to me, as yet extend quite up to the palatal of the same side. The nasal bones, situated further forwards, rested on the cartilaginous roofs of the nasal sacs (Nasendächer), and consisted of two very thin plates, proportionally much shorter than in the adult. The maxillæ and premaxillæ, on account of the small dimensions of the snout, attained also a much less relative length than at a more advanced time of life. The palatine and facial portions of each were represented by easily detached plates; between them, and occupying the place of the future alveolus, was a groove; according to my observation they nowhere came in contact.[2] The facial portion of each was tolerably thick, but very loose and spongy; the palatine portions thin, but much more compact. The palatine processes, both of the premaxillæ and maxillæ, had united so closely along almost their whole length, that they formed a complete roof to the palate, separating the cavities of the mouth and nose. Further back the partition was not yet formed, but the palatal roof was widely open. The intervening space, through which could still be seen the lower edge of the inter-orbital septum covered with the mucous membrane of the mouth, was narrowest at its middle, broadest at its hinder end, and bounded in its whole length by the palatals. The palatals themselves appeared as two simple narrow slips of bone; they must, therefore, increase greatly in breadth subsequently, in order to form the two horizontal flat plates, which ultimately, along their whole length, lie close together, in the same plane with the palatine portions of the premaxillæ and maxillæ. A further change is, that each palatal sends out from its posterior half a long lamina upwards and inwards, which, arching round again in a downward direction, unites with a corresponding process of the fellow palatal. Later on, the posterior halves of the palatals develop two canals running close together as prolongations of the nasal passages. In the embryo of the

[1] The descending process of the pre-frontal.

[2] That is, the palatine was nowhere in contact with the facial portion.

Alligator no trace was visible of these palatine lamellæ, which in Crocodilia contribute a still further prolongation to the already much produced nasal passages, nor were the palatine processes of the pterygoids yet apparent. The pterygoids first appeared as simple and very slender plates of bone, attached very slightly to the base of the cranium. They resembled in form and position the pterygoids of the young and adult *Alligator lucius*, apart from their palatine processes. They were, however, somewhat narrower in proportion to their length, more pointed in front, and more decidedly arched. The paired bones, which connect the pterygoids with the jugals and maxillæ (transverse bones of Cuvier) [1] were barely perceptible as yet; they were extremely small, and only loosely attached to the other bones just named.

[1] Transpalatines of the foregoing description.

ERRATUM.

P. 12, *for* "cranio-spinal" *read* "cerebro-spinal."

THE END.

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